THE FIRST FOSSIL PYGOPOD (SQUAMATA, GEKKOTA), AND A REVIEW OF MANDIBULAR VARIATION IN LIVING SPECIES

MARK N. HUTCHINSON

The snake-like Australian pygopod lizards (Pygopodidae in traditional taxonomies) show considerable variation in mandibular and dental structure, correlated with dietary specialisation in several genera. Following a review of this variation, a fully toothed Miocene dentary from Riversleigh, northwestern Queensland, is identified as a pygopod, the first in the fossil record. *Pygopus hortulanus* sp. nov. is specifically distinguishable from living *Pygopus* by tooth morphology and proportions of the symphysial region of the dentary. □ *Pygopods, lizards, osteology, fossils, Miocene.*

Mark N. Hutchinson, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia; 4 December 1996.

One of the most distinctively Australian squamate radiations is a group of snake-like, virtually limbless lizards, variously known as flap-footed lizards or snake-lizards (Bustard, 1970). These have no external trace of forelimbs while hind limbs are reduced to fin-like flaps on each side of the vent (Kluge, 1974; Shea, 1993). There are 35 species in 8 genera (Greer, 1989; Shea, 1991; Cogger, 1992). All are restricted to Australia and New Guinea.

Flap-footed lizards have long been regarded as forming a distinct family, the Pygopodidae, closely related to the Gekkonidae (Underwood, 1954, 1957). It has been suggested that the sister group of Pygopodidae is not all Gekkonidae, but only the Australian Diplodactylinae, or some part of that subfamily (Kluge, 1987; King & Mengden, 1990). Acceptance of this phylogenetic hypothesis (dissenting views exist; see Estes et al., 1988) would mean changes in taxonomy, with the diplodactylines becoming a subfamily of the Pygopodidae, as proposed by Kluge (1987) or the pygopodids becoming a subfamily of the Gekkonidae (Bauer, 1990). Pending a concensus view I use Underwood's (1957) contraction of their traditional family name, 'pygopods', as an informal collective term.

Pygopods show considerable ecological and morphological diversity. *Aprasia*, *Pletholax* and *Ophidiocephalus*, exhibit fossorial adaptations and behaviour (Kluge, 1974; Ehmann, 1981; Shea & Peterson, 1993). However, *Pletholax gracilis* and at least some species of *Aprasia* are regularly active on the surface by day (Shea & Peterson, 1993; pers. obs.). Species in the largest genus, *Delma*, and that regarded by Kluge (1974;

1976) as most generally primitive, *Pygopus*, as well as *Lialis*, *Aclys* and *Paradelma*, are surface-dwellers (Wilson & Knowles, 1988; Greer 1989). While most pygopodids appear to be active foragers feeding on invertebrates, the two species of *Lialis* are ambush predators of scincid lizards (Patchell & Shine, 1986a, b; Murray et al., 1991).

The mandibular and dental anatomy of pygopods is varied, and at least partly correlated with the ecological diversity just mentioned. The one overview of pygopod osteology attempted (Stephenson, 1962) gave scant attention to the mandible. Kluge (1974, 1976) employed some mandibular characters in his analysis of the clade, and Rieppel (1984) noted some correlations between anatomy and miniaturisation in *Aprasia* and *Pletholax* when compared to *Pygopus*. Parker (1956) noted sexual dimorphism in *Aprasia*, in which only males have premaxillary teeth.

Australia's fossil lizard fauna is poorly known (Estes, 1983a, b; Covacevich et al., 1990; Hutchinson, 1992); no fossil pygopods have been identified. Fossils are essential for establishing a minimum estimate of the time a taxon has inhabited an area and of the time since the taxon first evolved. If pygopods are the sister group of diplodactylines, especially the Diplodactylini (Kluge, 1987), then it is likely that their differentiation occurred in Australia and should be recorded in the Australian fossil record. This paper is the first report of a fossilised pygopod.

MATERIALS AND METHODS

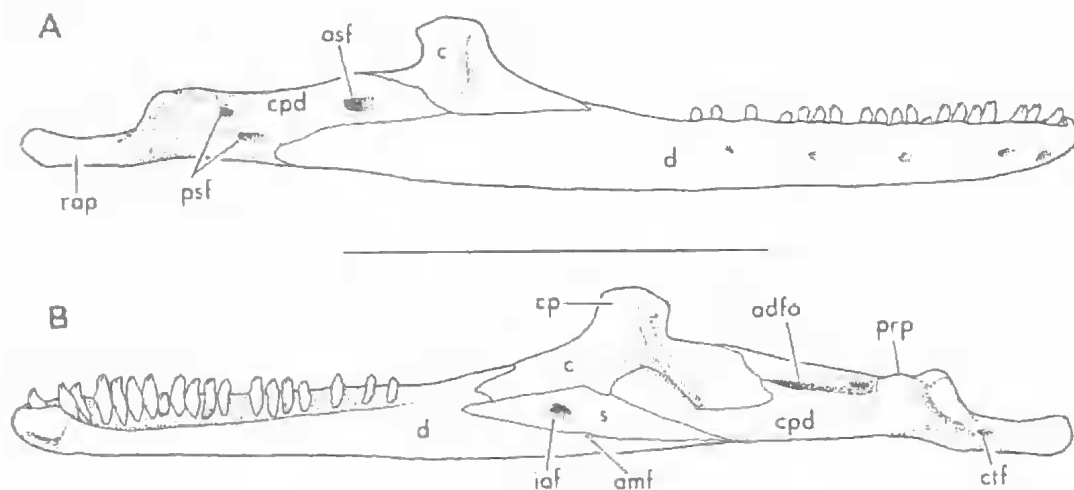Dried skeletons (21 species in 8 known genera; Appendix) were examined to assess interspecific

FIG. 1. Labial (A) and lingual (B) views of the right mandibular ramus of a pygopodid lizard, *Delma fraseri* (SAMAR22911, Coomalbidgup, W.A.) showing major features. Abbreviations: adfo=adductor (=Meckelian) fossa; amf=anterior mylohyoid foramen; asf=anterior surangular foramen; c=coronoid; cp=dorsal process of coronoid; cpd=compound bone - fused prearticular, surangular and articular; ctf=foramen for chorda tympani; d=dentary; iaf=inferior alveolar foramen; prp='prearticular process' (medial articular process of the surangular); psf=posterior surangular foramina; rap=retroarticular process; s=splenial. Scale=5mm.

variation in the sutural relationships of the mandibular bones, positions of foramina, tooth number and tooth morphology. With the exception of *Pygopus*, this sample did not permit study of intraspecific variation. Unless otherwise specified, the descriptions refer to the anatomy as seen in intact mandibles. Outgroups used to infer derived character states are diplodactylines as the sister group of pygopods, gekkonines the sister of these two and other scleroglossans as the most distant outgroup (Estes et al., 1988).

PYGOPOD MANDIBLE (Fig. 1).

The dentary is the largest bone of the pygopod mandible. It consists of the tooth-bearing body of the bone and a relatively long, posteriorly directed angular process that covers much of the labial and ventral surface of the mandible. Pygopods share with other gekkonoids and members of several other families the complete obliteration by dentary overgrowth of the groove for Meckel's cartilage, but differ, at least from all diplodactylines examined, in that the angular process extends on the labial surface of the mandible to well behind the coronoid (the dentary also extends posteriorly to a marked degree in the gekkonine *Paroedura*, Kluge, pers. comm.). The dentary of diplodactyline and gekkonine geckoes

is generally more slender and incurved than that of pygopods and the angular process terminates at about the level of the coronoid. 3-8 mental foramina open along the labial surface of the dentary, the series generally extending posteriorly to 1/2-3/4 the length of the tooth row. There is no posterior extension of the bony internal septum separating the Meckelian cartilage from the inferior alveolar nerve; bony separation is limited to the immediate vicinity of the mental foramina. Estes et al. (1988) described this character (their number 56) in terms which emphasised that a vertically-oriented, posteriorly extended intramandibular septum is well-developed in anguimorphs, but failed to note that it occurs to almost the same extent in lygosomine skinks (Shea & Hutchinson, 1992, fig. 3).

Adult geckoes typically have large numbers of small dentary teeth (Bauer & Russell, 1990; Kluge & Nussbaum, 1995); in a sample of 9 diplodactyline, 1 sphaerodactyline and 14 gekkonine genera, dentary counts ranged from 25 (*Phelsuma madagascariensis*) to 62 (*Saltuarius salebrosus*), with a mean of 40.2 (Edmund, 1969; pers. obs.). In adult *Delma* and *Aclys* tooth number is very much like that of diplodactyline and gekkonine geckoes, typically in the range 25-35. Reductions to 24 or fewer, or increases to 50 or more are therefore likely to be apomorphic

(Kluge, 1976). Diplodactylines and gekkonines usually have slender, upright teeth with acute crowns bearing a pair of pointed apical cusps separated by a groove (Sumida & Murphy, 1987). Teeth with this morphology occur in some pygopods (*Delma* and *Aclys*), and are probably plesiomorphic for the group. Within pygopods there is marked intergeneric variation, including robust, upright or slightly recurved teeth, less robust but more strongly recurved teeth, or very small teeth with compressed, sharp-edged crowns. All retain an apical groove, but the bicuspid structure is largely lost, the labial cusp enlarging to become the tooth apex, while the lingual cusp all but disappears. In *Lialis* tooth crowns are so compressed that the apical groove is faint and only discernible in unworn teeth.

The coronoid consists of a laterally compressed dorsal process, an anteriorly-directed dentary process and a posterior process. The dentary process is bifurcated and clasps the dentary bone behind the end of the tooth row both labially and lingually. On the lingual face of the mandible, the anterior extremity of the dentary process terminates posterior to, coextensively with, or anterior to the front of the splenial, the latter 2 character states being apomorphic with respect to other gekkonoids and other lizards. The posterior process of the coronoid extends to the anterior extremity of the Meckelian fossa. The form of the dorsal process varies from tall and fin-like in several genera to very low in *Lialis* (Kluge, 1976). A well-developed dorsal process is the rule in geckoes and other lizards and is likely to be plesiomorphic for pygopods.

The splenial is reduced in all pygopods compared to the development seen in diplodactylines and other geckoes, usually failing to extend anteriorly beyond the level of the distal two or three teeth. In most pygopods the splenial is further reduced in length or depth. The splenial is completely absent in *Aprasia* (pers. obs.; Parker, 1956; 'very slight', Stephenson, 1962). The splenial, when present, completely surrounds (as in diplodactylines) the inferior alveolar foramen and bears a notch for the anterior mylohyoid foramen on its ventral suture with the dentary.

Like the majority of geckoes (Kluge, 1987), pygopods lack a distinct angular. The splenial in *Delma* and *Pygopus* has a posteriorly extending process that separates the dentary and prearticular, as would an angular, suggesting that the angular has been lost via fusion with the splenial.

The surangular is fused labially and posteriorly with the fused prearticular-articular in adult

pygopods, but is completely distinct in juveniles (*Delma molleri*, *Lialis burtonis* and *Pygopus lepidopodus*). In adults of most genera a suture persists on the lingual face of the mandible running anteriorly from the Meckelian fossa; in intact mandibles this suture may be concealed by the coronoid. 3 foramina are usually present on the labial surface of the surangular. The anteriorly directed opening of the anterior surangular foramen lies on the labial surface on or just posterior to the point of intersection of the sutures between the coronoid, dentary and surangular. 2 other foramina usually lie towards the posterolabial region of the surangular, but there is intergeneric variation. In some pygopods there may be only a single foramen, as in diplodactylines, but in most there are 2. The 2 openings may be close together, or moderately separated, and the more posterodorsal of the 2 may itself be subdivided.

Most lizards have only a single posterior surangular foramen, and so the additional (more anterior) foramen must be identified. Kluge (1967) and Grismer (1988) designated the more ventral of the posterior foramina as the posterior mylohyoid and the more dorsal as the posterior surangular foramen. My survey of gekkonoid mandibular variation suggests that this interpretation is incorrect.

The posterior mylohyoid nerve innervates the throat musculature (Camp, 1923; Poglayen-Neuwall 1954) and typically exits through a medially or ventromedially directed foramen in the angular bone. While the angular is absent in most gekkonoids (Kluge, 1987) some of those examined (the gekkonines *Gekko*, *Phelsuma* and *Phyllodactylus* [=*Christinus*]) retain a small foramen on the dentary-splenial suture in the expected topographic position of the posterior mylohyoid foramen. Other gekkonines and other gekkonoids examined, including all pygopods, lack a foramen in this position.

The foramen identified by Kluge (1967) and Grismer (1988) as the posterior mylohyoid opens on the labial surface of the mandible and runs through to open lingually into the Meckelian fossa. This foramen thus follows the course of the posterior surangular foramen of other lizards, and it too transmits a branch of the mandibular nerve to the adductor (pterygoideus) musculature (pers. obs.). The foramen and nerve are remote from the throat musculature which, by definition, the posterior mylohyoid supplies. It therefore seems to me more probable that the additional foramen on the labial surface of the surangular in pygopods and other gekkonoids represents a duplication of
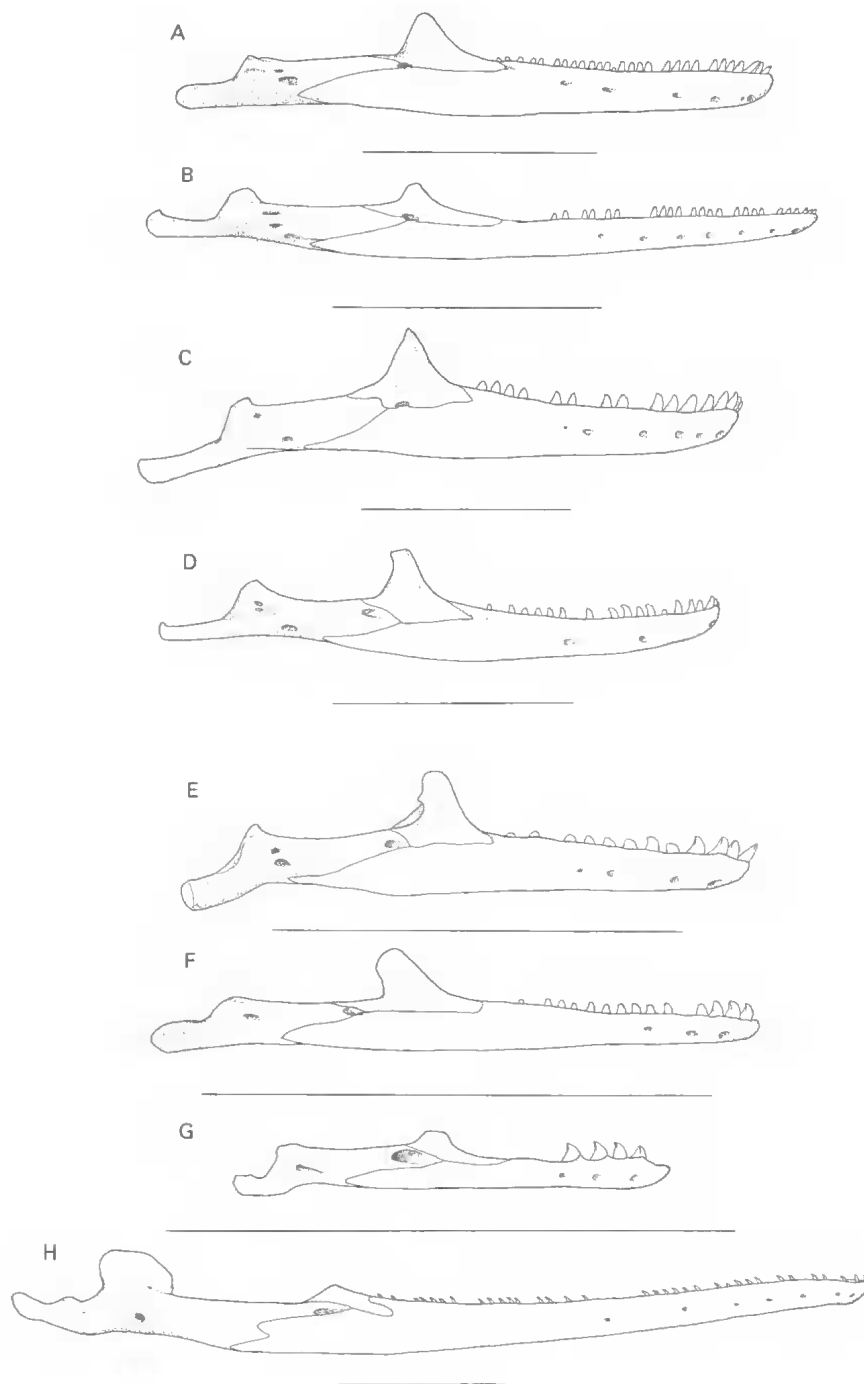
FIG. 2. Labial views of right mandibular ramus of the 8 pygopodid genera. A, *Delma inornata* (SAMAR22408, no data); B, *Aclys concinna* (SAMAR38060, Badgingarra National Park, W.A.); C, *Pygopus nigriceps* (SAMAR21029, no data); D, *Paradelma orientalis* (QMJ30250, Cracow, Qld); E, *Ophidiocephalus taeniatus* (SAMAR28365, Abminga, S.A.); F, *Pletholax gracilis* (SAMAR38061, Jandakot, W.A.); G, *Aprasia striolata* (SAMAR35569, Mylor, S.A.); H, *Lialis burtonis* (NMVD15399, Warby Ranges, Vic.). Scales=5mm.
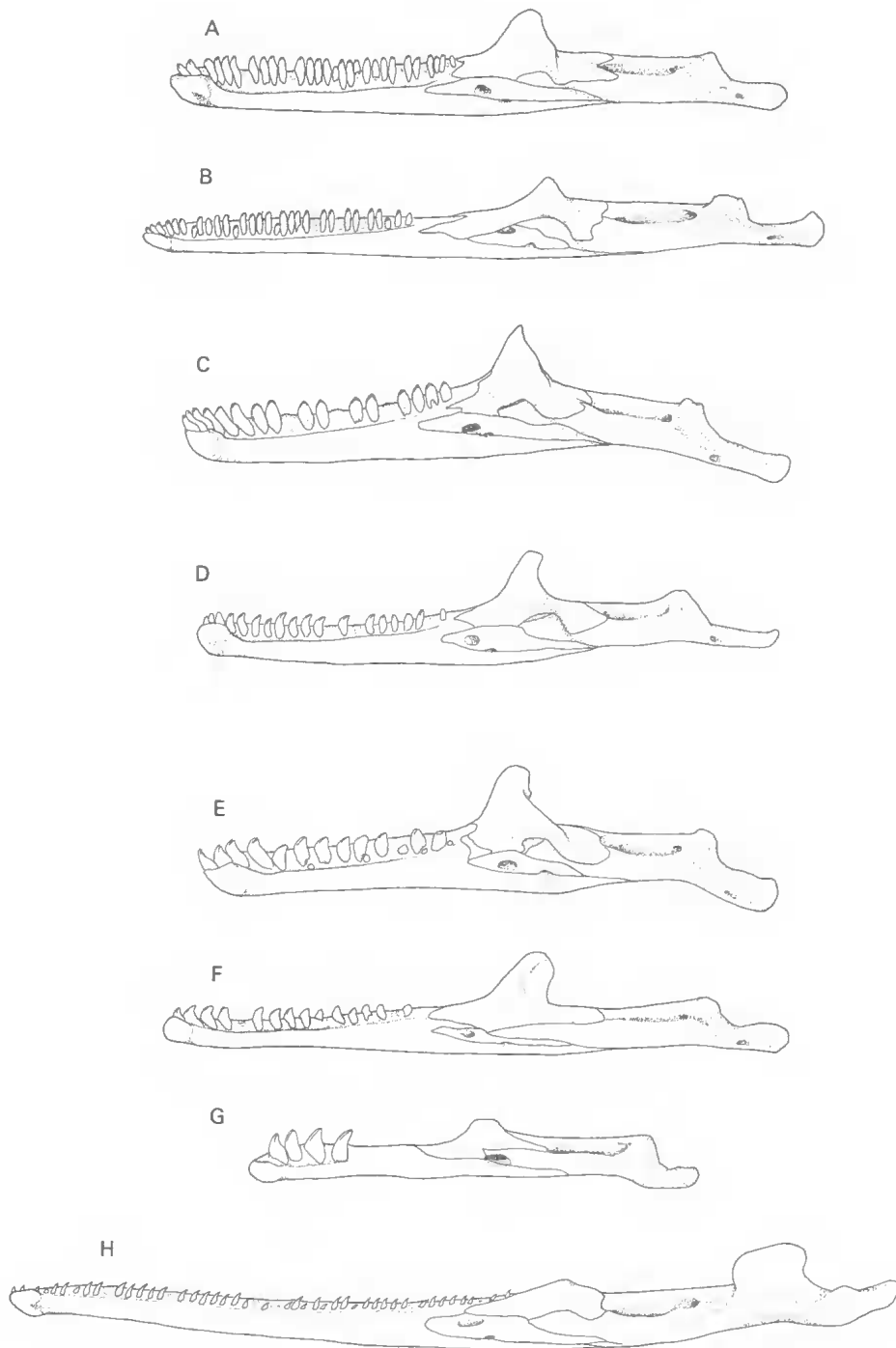
FIG. 3. Lingual views of same specimens in Fig. 2, drawn to same scales.

the posterior surangular foramen, not a displaced posterior mylohyoid.

The fused prearticular-articular together with the surangular constitutes the posterior 1/3 of the pygopod mandible. As in diplodactylines and other gekkonoids the articulating facet is oriented to face posterodorsally rather than dorsally, resulting in a marked 'step' down from the level of the upper edge of the adductor fossa to the level of the retroarticular process. The latter structure is variable intergenerically in its shape (spoon-shaped to rod-like) and the degree of medial or ventral inflection (Kluge, 1976). A foramen for the n. chorda tympani opens on the dorsolingual aspect of the base of the retroarticular process. The posterior region of the Meckelian fossa, which contains the internal opening for the posterior surangular foramen, may be demarcated from the anterior region.

MANDIBULAR VARIATION IN LIVING PYGOPODS

DELMA. This genus has the most generally 'gecko-like' mandibles. However, there is significant variation within the genus in proportions, tooth crown shape, size of splenial and other features. *Delma fraseri* (Fig. 1) and *D. inornata* (Figs 2A, 3A) show some of this variation, with the latter species tending to retain more plesiomorphic features than the former. The pygopod synapomorphy of extensive posterior extent of the dentary on the labial surface is present in all *Delma* , but the teeth are numerous, with unmodified (e.g. *D. impar, D. inornata, D. nasuta*) or slightly expanded crowns (e.g. *D. fraseri, D. mitella*). Whether this is inter- or intraspecific variation will require a more extensive survey. Tooth crowns retain the bicuspid morphology of diplodactyline geckoes. The dentary is moderately slender and the splenial little reduced, although it usually fails to extend anteriorly as far as the posteriormost tooth (*D. inornata* specimens showed intraspecific variation, the splenial failing to reach the tooth row in NMVD15448, reaching the second-last tooth in SAMAR35570 and extending as far as the sixth-last in SAMAR22408, Fig. 2A). The posterior surangular foramina are moderately to narrowly separated (variable both inter- and intraspecifically). The relatively unspecialised dentition is associated with a generalised arthropod diet (Shine & Patchell, 1986a; Coulson, 1990).

ACLYS (Figs 2B, 3B). In general the mandible of

this genus is an elongate version of *Delma's.* Elongation of the jaw occurred by lengthening of the region between the tip of the coronoid process of the dentary and the posterior end of the tooth row, with hypertrophy of the lingual ramus of the anterior process of the coronoid reducing the exposure of the splenial and widely separating it from the tooth row. Height of the dorsal process of the coronoid is reduced relative to most *Delma* and the medial articular process (Fig. 1) of the surangular is elevated, both trends foreshadowing the extensive coronoid flattening and surangular elevation of *Lialis.* The derived features of the jaw of *Aclys* are all seen, although not to the same degree, in some *Delma*, especially those with more elongate skulls such as *D. butleri* and *D. nasuta.*

PYGOPUS (Figs 2C, 3C, 4B, 4D). The mandibles of the two species placed in this genus are very similar to one another, and probably indistinguishable. The form of the mandible is apomorphic with respect to that of *Delma* in being shorter and deeper. The dentition is also apomorphic, the teeth being fewer (<25), much more robust, and with sharp, tapering, recurved crowns. The tooth crowns retain a pronounced apical groove, but the typical gekkonoid bicuspid structure is reduced, with the labial cusp being the principle tooth apex while the lower, lingual cusp is little more than the acute-angled inner margin of the apical groove. The mandible is more plesiomorphic than most *Delma* in that the splenial extends forward to underly the posteriormost teeth. The posterior surangular foramina are moderately to widely separated (intraspecifically variable). The genus is characterised by a pronounced mesio-distal decrease in tooth size, the mesial teeth (second to fifth) being 30-40% taller than the mid-dentary teeth (tenth to twelfth). The enlarged teeth at the front of the jaw are somewhat procumbent and are supported by a deep symphysial region. Pianka (1986) described *P. nigriceps* as a scorpion specialist, and Patchell & Shine (1986a) found that the major prey of *P. lepidopodus* were mygalomorph and lycosid spiders. Possibly the relatively powerful front teeth are adaptations for rapidly disabling such potentially dangerous prey.

PARADELMA (Figs 2D, 3D). This monotypic genus, like *Pygopus*, has a reduced tooth number (21) compared with *Delma* but the teeth are distinctive, being more slender than in *Pygopus* and having recurved crowns. The tooth apices are like

those of *Pygopus* in that the apical groove is present but the lingual cusp is barely developed. Compared with *Pygopus*, the jaw is less robust and more bowed. The diet is unknown.

OPHIDIOCEPHALUS (Figs 2E, 3E). The jaw of this small fossorial form is relatively robust, short and deep, similar in proportions to that of *Pygopus*, but is apomorphic in several characters. The splenial is greatly shortened and shifted posteriorly compared with *Pygopus*. The single jaw examined is distinctive in that the lingual ramus of the anterior process of the coronoid is reduced, exposing the bone beneath. Based on the position of the prearticular-surangular suture exposed below the dorsal process of the coronoid, this anteriorly exposed bone is the surangular. The posterior surangular foramina are narrowly separated. The teeth are similar in to those of *Pygopus*, but are fewer in number (13-15 in adults versus 17-24 in hatchling to adult *Pygopus*) and have moderately recurved crowns. Recorded prey indicates a relatively generalised arthropod diet (Ehmann, 1981).

PLETHOLAX (FigS 2F, 3F). The jaw is long and slender, but with a well-developed dorsal process of the coronoid. Tooth counts are below 20 (Kluge, 1976), with the mesial teeth relatively robust, pointed and slightly recurved while the more distal teeth are markedly reduced in size. The splenial is reduced to a narrow splint but still encloses the inferior alveolar foramen and forms the dorsal margin of the anterior mylohyoid foramen. There is a single posterior surangular foramen. Shea & Peterson (1993) found that most guts of this species contained little chitinous material but often included short cut lengths of grass, consistent with digestion from the bodies of insect prey. They suggested the most likely diet was poorly-sclerotised, readily digested prey such as termites. Ehmann (1993) suggested that *Pletholax* is a nectar feeder. The weak jaws and small, widely spaced teeth suggest it would be unlikely to deal effectively with the tough exoskeletons of typical invertebrate prey.

APRASIA (Figs 2G, 3G). The mandible has only 3 elements; dentary, coronoid and a compound bone representing the remainder; the splenial is absent, whether through loss or fusion is unclear. The inferior alveolar foramen lies on the suture between the anterior extremity of the compound bone and the dentary. The posterior surangular foramen is single. The dorsal process of the coronoid is reduced and the retroarticular process is abbreviated. The teeth are very greatly reduced in number, restricted to a patch of 3-4 relatively robust, pointed, recurved teeth situated close to (but not on) the symphysis. The diet is restricted to the eggs, larvae and pupae of ants (Webb & Shine, 1994). The mandibular and dental anatomy of *Aprasia* is thus convergent to some extent on that of ant-eating scolecophidian snakes, which also have weak, almost edentulous jaws save for a few teeth in the upper (Typhlopidae) or lower (Leptotyphlopidae) mandible.

LIALIS (Figs 2H, 3H). This genus has a highly derived mandibular morphology. The dentary is greatly attenuated, with many (to over 60) small, recurved, sharply pointed teeth having ligamentous basal attachments (*L. burtonis*, Patchell & Shine, 1986b; *L. jicari*, G. Shea, pers. comm.). Other peculiarities include the greatly reduced height of the coronoid and a peculiar fan-like medial articular process of the surangular ascending well above the level of the articular region, and higher than the coronoid. Functionally this braces the jaw against the quadrate ramus of the pterygoid, preventing lateral displacement of the jaw when the mouth is open. Along with these apomorphies, *Lialis* retains a plesiomorphic, relatively large, anteriorly extending splenial. The posterior surangular foramen is single or double. The wide gape and specialised dentition are related to the obligate lizard-eating (especially skink-eating) habits of this genus (Patchell & Shine, 1986b).

SYSTEMATICS

Infraorder GEKKOTA Cuvier, 1817
Family PYGOPODIDAE

Pygopus Merrem, 1870

TYPE SPECIES. *Bipes lepidopodus* Lacepede, 1804

Pygopus hortulanus sp. nov. (Figs)

ETYMOLOGY. Latin *hortulanus*, of or belonging to a garden; alluding to the Neville's Garden Site.

MATERIAL. Holotype QMF16875 (Fig. 4), a right dentary preserving the complete tooth row and symphysial region but minus the angular process from early Miocene, System B (Archer et al., 1994), Neville's Garden Site on D Site Plateau at Riversleigh, NW Queensland; the site is interpreted as representing an accumulation in a pool close to a cave entrance.
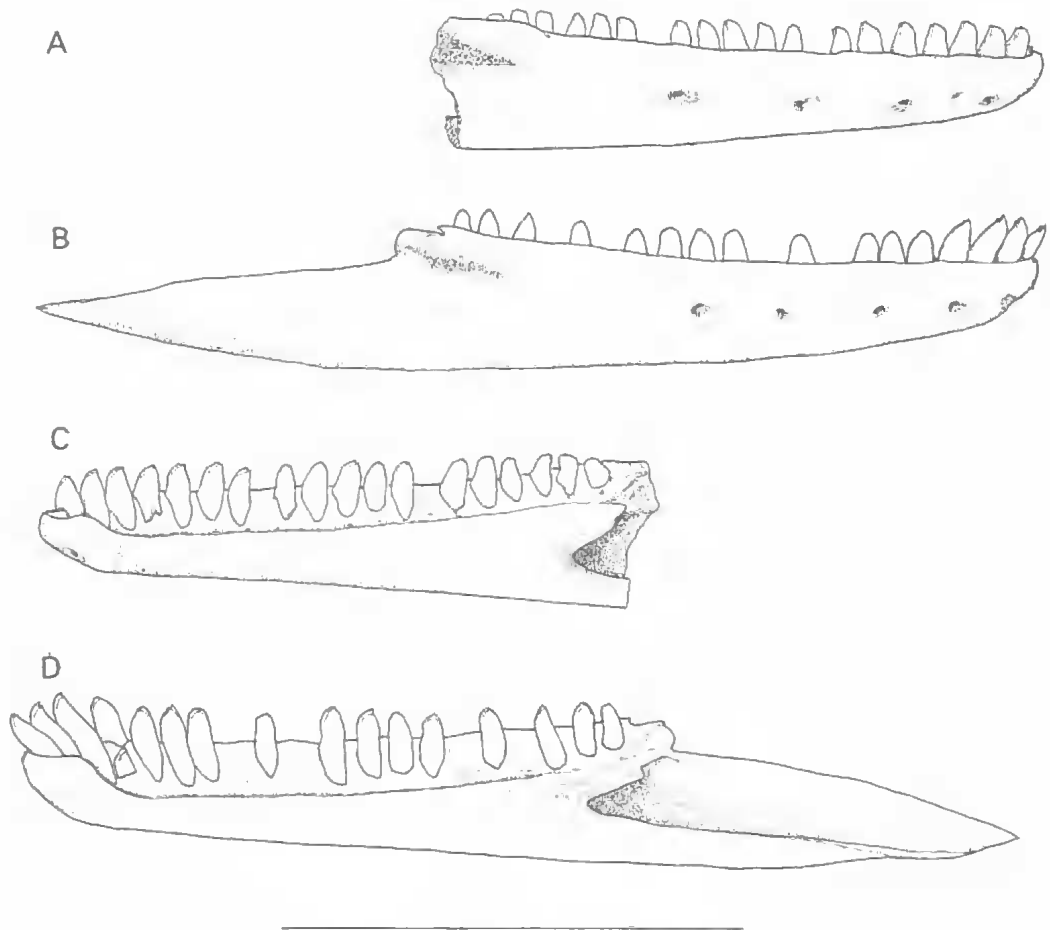
FIG. 4. Comparison of the dentaries of *Pygopus hortulanus* SP. NOV. (A and C, QMF16785) and *P. lepidopodus* (B and D; SAMAR38928). A-B, labial views; C-D, lingual views. Note larger mesial (anteriormost) teeth and deeper symphysis in *P. lepidopodus*. Scale=5mm.

DESCRIPTION. Right dentary, complete and undamaged except for the absence of the angular process posterior to the level of the end of the tooth row. Dental arcade in occlusal view straight from distal tooth anteriorly to about seventh tooth (counting mesiodistally), then curving gently mesially. Lingual rim of dental sulcus distinct, rounded in cross-section. Groove for Meckel's cartilage completely obliterated by overgrowth of dentary. Intramandibular septum not extended posteriorly. In labial view, acute-angled splenial notch extending to level of penultimate (twentieth) tooth, and superficial facet for anterior extension of splenial extending as far as seventeenth tooth. Wedge-shaped facet for anteroventral extremity of coronoid incised into posterior margin between dorsal edge of splenial notch and last

tooth. Labial surface with 5 mental foramina, last level with fourteenth tooth. Shallow fossa on labial surface tapering anteriorly from posterodorsal margin of dentary. Total length 6.0mm; depth at level of last tooth 1.4mm (tooth excluded).

Tooth loci 21. Counting from mesial to distal, all but first (broken), ninth and fifteenth (empty) with intact teeth. Twentieth tooth lost subsequent to preparation of Fig. 4. Length of tooth row 5.2mm.

Teeth robust, 2.5-3 times as high as wide, crowns tapering rapidly to sharp points. Well-defined groove traversing each tooth crown, setting off weak second apical point, lower and lingual to main tooth apex. Tooth crowns slightly incurved. Teeth reducing gradually in size from

mesial to distal, but anteriormost teeth only slightly larger than mid-dentary teeth.

REMARKS. Identification of the fossil as a gekkonoid is based on apomorphic features: 1) obliteration of the groove for Meckel's cartilage by overgrowth of the dentary, 2) apex of the splenial notch level with the posterior end of the tooth row, with a narrow tongue of the splenial extending forward over the lingual face of the dentary below the tooth row, and 3) mesial (i.e. anteriormost) teeth largest (rather than mid-dentary teeth).

Many Australian skinks (Scincidae) also have the Meckelian groove obliterated by the dentary, but in these the splenial notch extends well forward under the tooth row (the tiny *Notoscincus*, tooth row <3mm, is an exception), and scincid dentaries with a closed Meckel's groove all have a vertically oriented, posteriorly extended intramandibular septum. Skinks, unlike gekkonoids (Bauer, 1990; Bauer & Russell, 1990), have the mid-dentary teeth larger than the mesial teeth. Scincid dentaries also have a pronounced coronoid process on the labial surface (Estes, 1983); although this part of the specimen is incomplete, existing outlines indicate that very little of this region is lost and that there was scarcely any development of this process. The only other lizard families in which dentary obliteration of the Meckelian groove occurs are the Xantusiidae (all), many Gymnophthalmidae and many iguanians (Presch, 1980; Estes et al., 1988; Etheridge & de Queiroz, 1988; MacLean, 1974). These can be excluded on the basis of tooth crown shape (McDowell & Bogert, 1954; Sumida & Murphy, 1987; MacLean, 1974; Etheridge & de Queiroz, 1988), and having mid-dentary teeth larger than mesial teeth.

Among gekkonoids, only pygopods have the stout, straight dentary shape, low dentary tooth counts and teeth of the robust form seen in *P. hortulanus*.

Pygopus hortulanus shows two seemingly derived character states within pygopods, the relatively short, deep dentary and the fewer robust teeth. These relate it not only to *Pygopus* but also *Ophidiocephalus*. The fossil is plesiomorphic with respect to *Ophidiocephalus* in straighter tooth crowns, more teeth and greater anterior extent of the splenial. It is plesiomorphic with respect to *Pygopus* perhaps in the less enlarged mesial teeth and (?correlated) shallower symphysial region. Alternatively the more even tooth row of *P. hortulanus* could be interpreted as autapomorphic, because enlarged anterior teeth are common in pygopods. The placement of the species in *Pygopus* rather than *Ophidiocephalus* reflects the fewer specialisations shared with *Ophidiocephalus* than with *Pygopus*.

The cladistic analysis of intergeneric relationships reported by Kluge (1974, 1976) not only concluded that *Pygopus* is the most primitive extant genus but also placed *Pygopus* as a grade group at the base of the pygopod radiation and suggested that *Paradelma orientalis* is more closely related to *Pygopus nigriceps* than the latter is to *Py. lepidopodus*. The placement of the fossil in *Pygopus* could therefore be taken to mean only that the fossil is a plesiomorphic pygopod. However, the short, deep dentary and robust teeth of *Pygopus* are probably apomorphic in pygopods, and I therefore maintain the concept of this genus employed by Cogger (1985), Greer (1989) and Shea (1993).

This early Miocene pygopod is consistent with Kluge's (1987) suggestion that pygopods evolved on the Australian continent subsequent to a Late Cretaceous vicariant event isolating the ancestral diplodactyline-pygopod stock. This find, with its apomorphic teeth, is not a generalised ancestral pygopod, implying the origins of the group must be older than the Miocene.

Archer et al. (1989; 1995) suggested that the Miocene environment of Riversleigh was primarily tropical closed forest, an assessment supported by many genera in Systems B and C whose living representatives are restricted to closed forest environments. Megirian (1992) suggested that sedimentological evidence argued for a more arid climate with any rainforest limited to water courses. Creaser (this volume) reports that sediment patterns regarded by Megirian as being confined to arid depositional environments occur today in mid-montane New Guinea.

No modern pygopod inhabits rainforest, although *Lialis* and some *Delma* (Shea, 1987) inhabit vine scrubs and eucalypt forest on the margins of rainforest. The presence of *P. hortulanus* in System B could be interpreted to indicate either that there were drier, open patches nearby, or that *P. hortulanus* was a rainforest-dweller with no living analogue.

ACKNOWLEDGEMENTS

LITERATURE CITED

ARCHER, M., GODTHELP, H., HAND, S. J. & MEGIRIAN, D. 1989. Fossil mammals of Riversleigh, northwestern Queensland: a preliminary overview of biostratigraphy, correlation and environmental change. Australian Zoologist 25: 29-65.

ARCHER, M., HAND, S. J. & GODTHELP, H. 1994. Riversleigh. 2nd ed. (Reed: Sydney).

1995. Tertiary environments and biotic change in Australia. Pp. 77-90. In Vrba, E.S., Denton, G.H., Partridge, T.C. & Burckle, L.H. Paleoclimate and evolution, with emphasis on human origins. (Yale University Press: New Haven).

BAUER, A. M. 1990. Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). Bonner Zoologisches Monographien 30: 1-217.

BAUER, A.M. & RUSSELL, A.P. 1990. Dentitional diversity in *Rhacodactylus* (Reptilia: Gekkonidae). Memoirs of the Queensland Museum 29: 311-321.

COGGER, H.G. 1992. Reptiles and amphibians of Australia. 5th ed. (Reed: Sydney).

COULSON, G. 1990. Conservation biology of the striped legless lizard, (*Delma impar*), an initial investigation. Arthur Rylah Institute for Environmental Research Technical Report 106: 1-40.

COVACEVICH, J., COUPER, P., MOLNAR, R.E., WITTEN, G. & YOUNG, W. 1990. Miocene dragons from Riversleigh: new data on the history of the Family Agamidae (Reptilia: Squamata) in Australia. Memoirs of the Queensland Museum 29: 339-360.

EDMUND, G. 1969. Dentition. Pp. 117-200. In Gans, C., Bellairs, A.d'A. & Parsons, T.S. Biology of the Reptilia, vol. 1, Morphology A. (Academic Press: London).

EHMANN, H. 1981. The natural history and conservation of the bronzeback (*Ophidiocephalus taeniatus* Lucas & Frost) (Lacertilia, Pygopodidae). Pp. 7-13. In Banks, C. & Martin, A.A. Proceedings of the Melbourne Herpetological Symposium. (Zoological Board of Victoria: Melbourne).

1993. Encyclopaedia of Australian animals: reptiles. (Australian Museum with Angus & Robertson: Sydney).

ESTES, R. 1983a. Encyclopedia of paleoherpetology, vol. 10A. Sauria terrestria, Amphisbaenia. (Gustav Fischer Verlag: Stuttgart).

1983b. The fossil record and early distribution of lizards. Pp. 365-398. In Rodin, A.G.J. & Miyata, K. Advances in herpetology and evolutionary biology. (Museum of Comparative Zoology, Harvard: Cambridge).

ESTES, R., DE QUEIROZ, K. & GAUTHIER, J. 1988. Phylogenetic relationships within Squamata. Pp. 119-281. In Estes, R. & Pregill, G. (eds), Phylogenetic relationships of the lizard families. (Stanford University Press:Stanford).

ETHERIDGE, R. & DE QUEIROZ, K. 1988. A phylogeny of Iguanidae. Pp. 283-368. In Estes, R. & Pregill, G. (eds), Phylogenetic relationships of the lizard families. (Stanford University Press: Stanford).

GREER, A.E. 1989. The biology and evolution of Australian lizards. (Surrey Beatty & Sons and the Royal Zoological Society of NSW: Sydney).

GRISMER, L. L. 1988. Phylogeny, taxonomy, classification and biogeography of eublepharid geckos. Pp. 369-469. In Estes, R. & Pregill, G. (eds), Phylogenetic relationships of the lizard families. (Stanford University Press: Stanford).

HUTCHINSON, M.N. 1992. Origins of the Australian scincid lizards: a preliminary report on the skinks of Riversleigh. The Beagle, Occasional Papers of the Northern Territory Museum of Arts and Sciences 9: 61-70.

KING, M. & MENGDEN, G. 1990. Chromosomal evolution in the Diplodactylinae (Gekkonidae: Reptilia). II. Chromosomal variability between New Caledonian species. Australian Journal of Zoology 38: 219-226.

KLUGE, A. G. 1967. Higher taxonomic categories of gekkonid lizards and their evolution. Bulletin of the American Museum of Natural History 135: 1-60.

1974. A taxonomic revision of the lizard family Pygopodidae. Miscellaneous Publications of the Museum of Zoology, University of Michigan 147: 1-221.

1976. Phylogenetic relationships in the lizard family Pygopodidae: an evaluation of theory, methods and data. Miscellaneous Publications of the Museum of Zoology, University of Michigan 152: 1-72.

1987. Cladistic relationships in the Gekkonoidea (Squamata, Sauria). Miscellaneous Publications

of the Museum of Zoology, University of Michigan 173: 1-54.

KLUGE, A.G. & NUSSBAUM, R.A. 1995. A review of African- Madagascan gekkonid lizard phylogeny and biogeography (Squamata). Miscellaneous Publications of the Museum of Zoology, University of Michigan 183: 1-20.

MACLEAN, W. P. 1974. Feeding and locomotor mechanisms of teiid lizards: functional morphology and evolution. Papeis Avulsos de Zoologia, Sao Paulo 27: 179-213.

MCDOWELL, S. B. & BOGERT, C. M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bulletin of the American Museum of Natural History 105: 1-142.

MURRAY, B.A., BRADSHAW, S.D. & EDWARD, D.H. 1991. Feeding behavior and the occurrence of caudal luring in Burton's pygopodid *Lialis burtonis* (Sauria: Pygopodidae). Copeia 1991: 509-516.

MEGIRIAN, D. 1992. Interpretation of the Miocene Carl Creek Limestone, northwestern Queensland. The Beagle, Occasional Papers of the Northern Territory Museum of Arts and Sciences 9: 219-248.

PARKER, H.W. 1956. The lizard genus *Aprasia*. Bulletin of the British Museum (Natural History), Zoology 3: 363-385.

PATCHELL, F.C. & SHINE, R. 1986a. Food habits and reproductive biology of the Australian legless lizards (Pygopodidae). Copeia 1986: 30-32.

PATCHELL, F.C. & SHINE, R. 1986b. Hinged teeth for hard bodied prey: a case of convergent evolution between snakes and legless lizards. Journal of Zoology, London 208: 269-275.

PIANKA, E.R. 1986. Ecology and natural history of desert lizards. (Princeton University Press: Princeton).

POGLAYEN-NEUWALL, I. 1954. Die Kiefermuskulatur der Eidechsen und ihre Innervation. Zeitschrift für wissenschaftliche Zoologie 158: 79-132.

PRESCH, W. 1980. Evolutionary history of the South American microteiid lizards (Teiidae: Gymnophthalminae). Copeia 1980: 36-56.

RIEPPEL, O. 1984. Miniaturization of the lizard skull: its functional and evolutionary implications. Pp 503-520. In Ferguson, M.W.J. (ed.), The structure, development and evolution of reptiles. Symposium of the Zoological Society of London 52: .

SHEA, G.M. 1987. Two new species of *Delma* (Lacertilia: Pygopodidae) from northeastern Queensland and a note on the status of the genus *Aclys*. Proceedings of the Linnean Society of N.S.W. 109: 203-212.

1991. Revisionary notes on the genus *Delma* (Squamata: Pygopodidae) in South Australia and the Northern Territory. Records of the South Australian Museum 25: 71-90.

1993. Family Pygopodidae. Pp 234-239. In Glasby,

C.J., Ross, G.J.B. & Beesley, P.L. Fauna of Australia. Vol 2A, Amphibia and Reptilia. (Australian Government Publishing Service: Canberra).

SHEA, G.M. & HUTCHINSON, M.N. 1992. A new species of *Tiliqua* from the early Miocene of Riversleigh, Queensland. Memoirs of the Queensland Museum 32: 303-310.

SHEA, G.M. & PETERSON, M. 1993. Notes on the biology of the genus *Pletholax* Cope (Squamata: Pygopodidae). Records of the Western Australian Museum 16: 419-425.

STEPHENSON, N.G. 1962. The comparative morphology of the head skeleton, girdles and hind limbs in the Pygopodidae. Zoological Journal of the Linnean Society 44: 627-644.

SUMIDA, S.S. & MURPHY, R.W. 1987. Form and function of the tooth crown structure in gekkonid lizards (Reptilia, Squamata, Gekkonidae). Canadian Journal of Zoology 65: 2886-2892.

TYLER, M.J., HAND, S.J. & WARD, V.J. 1990. Analysis of the frequency of *Lechriodus intergerivus* Tyler (Anura: Leptodactylidae) in Oligo-Miocene local faunas of Riversleigh Station, Queensland. Proceedings of the Linnean Society of N.S.W. 112: 105-109.

UNDERWOOD, G. 1954. On the classification and evolution of geckos. Proceedings of the Zoological Society of London 124: 169-492.

1957. On lizards of the family Pygopodidae. Journal of Morphology 100: 207-268.

WEBB, J.K. & SHINE, R. 1994. Feeding habits and reproductive biology of the Australian pygopodid lizards of the genus *Aprasia*. Copeia 1994: 390-398.

WILSON, S.K. & KNOWLES, D.G. 1988. Australia's reptiles. A photographic reference to the terrestrial reptiles of Australia. (Collins:Sydney).

APPENDIX

Pygopodid skeletal specimens examined: *Aclys concinna* SAMA R38060; *Aprasia inaurita* SAMA R14275; *A. pseudopulchella* SAMA R406A; *A. striolata* SAMA R35569, R41825; *Aprasia* sp. SAMA unregistered alizarin specimen; *Delma australis* SAMA R15958; *D. butleri* SAMA R14913, R16843A; *D. fraseri* SAMA R22911; *D. impar* NMV D15446; *D. inornata* SAMA R22408, R35570, NMV D15448; *D. mitella* AMS R65264 (partial dentary only); *D. molleri* SAMA R22540, R35572; *D. nasuta* SAMA R22517; *D. plebeia* QM J5891; *D. tincta* SAMA R15189A; *Lialis burtonis* SAMA R15882, R40031, QM J47481, NMV D15399; *L. jicari* SAMA R11441; *Ophidiocephalus*

taeniatus SAMA R28365 (mandible only); *Paradelma orientalis* QM J30250 (mandible only); *Pletholax gracilis* SAMA R38061; *Pygopus lepidopodus* SAMA R19604 (mandible only), R35571, R38924-28; *P. nigriceps* SAMA R1250, R21029.